PERGAMON

Continental Shelf Research 19 (1999) 911–928

CONTINENTAL SHELF RESEARCH

Predicting high-frequency upwelling: Spatial and temporal patterns of temperature anomalies on a Florida coral reef

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Received 12 October 1998; accepted 12 November 1998

Abstract

High-frequency measurements reveal a rapidly changing, highly variable temperature regime on the slope of Conch Reef, a coral reef in the upper Florida Keys, USA. Water temperatures 1 m above the reef were measured at 20 min intervals at 21 and 33 m depths from 1992 through 1997, for all of 1992 at 7 m depth and 1997 at 10 m. While the annual variation in daily-averaged temperatures was approximately 10°C in most years (Winter lows near 20°C to Summer highs near 30°C), temperature fluctuations as large as 6 to 10°C were recorded within individual days. Temperature variation is concentrated at semi-diurnal internal tidal frequencies, with a variety of mechanisms including internal tides, internal tidal bores, and cold water intrusions most likely related to variability of the Florida Current influencing high-frequency upwelling at this site. An analysis of extreme values in the long-term temperature records is used to predict return times for cold water upwelling events at depths of 7, 21, and 33 m. This analysis provides quantitative, seasonal estimates for among-depth differences in the extent of cool water pulsing. Return times for cooling events are shorter in May through September than in October through April, and decrease markedly with increasing depth on the reef slope. In Summer, the predicted median return times for a -3°C temperature anomaly are 136, 14, and 7 days at 7, 21, and 33 m depths, respectively. Predictable physical forcing arising from upwelling of cool water may be an important source of externally derived nutrients and suspended particles for this coral reef. The methods and results presented here should be applicable to a range of studies of temperature variation and nutrient dynamics in the Florida Keys and other regions. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Temperature extremes; Return times; Upwelling; Coral reefs

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PII: S0278–4343(99)00004–7

1. Introduction

Reef building (hermatypic) corals thrive primarily in warm, shallow, oligotrophic waters characterized by limited seasonal variation in physical conditions. While light, sedimentation, salinity, nutrient concentrations, and other physical variables such as water motion can all play important roles in shaping coral abundance and diversity patterns, it is water temperature that probably most limits the geographic distribution of coral reefs. Both upward and downward deviations from a relatively narrow range of temperatures can be problematic for individual coral colonies and for entire coral reefs. High temperatures above approximately 30–32°C can produce adverse effects ranging from bleaching associated with reversible loss of zooxanthellae, to death (Jokiel and Coles 1990; Glynn 1991, 1993). Low temperatures, due to persistent local upwelling, have long been invoked as an explanation for the limited coral reef development in the eastern tropical Pacific (e.g. Dana, 1843). A general consensus has since developed that corals are adversely affected by temperatures below approximately 18°C (Yonge 1940; Glynn and Wellington, 1983; Glynn and D'Croz, 1990; Veron, 1995). Cold water can produce a variety of effects in hermatypic corals including slowed calcification and growth rates, reduced feeding activity, release of zooxanthellae, and death (e.g., Mayor, 1916; Shinn 1966; Glynn and Stewart, 1973; Jokiel and Coles, 1977; Coles and Fadlallah, 1991). In addition, while the effects of rapidly fluctuating temperatures are poorly understood, both hot and cold shocks, even within acceptable physiological limits, can represent a significant source of stress to reef corals.

Cooling on coral reefs can occur in response to long-term seasonal climate variability, shorter term weather events such as passing atmospheric cold fronts accompanied by strong winds, and a variety of mechanisms of nearshore upwelling. Mechanisms of upwelling include Ekman transport in response to alongshore winds, nearshore current meanders and gyres (Atkinson, 1977; Lee et al., 1992, 1994, 1995), tidal jets (Wolanski, 1983, 1994), and forcing associated with internal tides, internal waves and internal tidal bores (Wolanski and Pickard, 1983; Wolanksi, 1994; Quinn and Johnson, 1996; Leichter et al., 1996). Cool, subsurface water generally contains elevated concentrations of dissolved nutrients (NO_3^-, PO_4^{3-}) relative to warmer, surface waters (Mann and Lazier, 1996). Both direct and indirect effects of changing nutrient concentrations can, therefore, accompany the potentially deleterious thermal effects of upwelling on reef corals. While high nutrient levels may negatively impact corals and stimulate overgrowth by benthic algae (Tomascik and Sander, 1987), intermittent upwelling may provide corals with important, and perhaps essential, nutrient pulses. Upwelling of cool water and nutrients has been invoked as a partial explanation of 'anomalous' high productivity and diversity on coral reefs despite the oligotrophic, low productivity waters in which reefs are generally found (Andrews and Gentien, 1982; Lapoint and Smith, 1987; Wolanski 1994). High-frequency upwelling driven by internal tidal bores has also been implicated as a source of suspended particles and planktonic larvae to a coral reef in the Florida Keys (Leichter, et al., 1998). Thus, temporal and spatial variability in upwelling near coral reefs may influence temperature variability and stress, the balance between locally- and remotely-derived nutrients, and the dynamics of benthic populations with dispersing larval stages.

This study was motivated as part of an on-going effort to understand thermal variability and stress, and nutrient dynamics, on a coral reef within the Florida Keys National Marine Sanctuary. Upwelling of anomalously cool water along the shelf of Florida and the Florida Keys has been variously linked to seasonal variability in coastal winds (Green, 1944; Taylor and Stewart, 1957), offshore meanders and gyres of the Florida Current resulting in near-bottom intrusions of subsurface water (Atkinson, 1977; Atkinson and Blanton, 1986; Lee et al., 1985, 1992, 1994), interactions between the cyclonic turn of the Florida Current in the Florida Straits and diverging bottom isobaths (Blanton et al., 1981; Smith, 1982, 1983), and cross-shelf, near-bottom transport by internal tidal bores (Leichter et al., 1996). While monthly mean temperatures along the Florida Keys reef track generally vary only 4–8° (winter lows 22–24°C, summer highs 28–30°C), upwelling events on a range of time scales from weeks to days to hours may produce extensive, high-frequency temperature variability within the seasonal temperature signal. The present study focuses on six years of nearly continuous, high frequency temperature data collected across a depth gradient on Conch Reef. These data represent the most extensive set of near-bottom temperature observations available for the Florida Keys, and, to our knowledge, for any coral reef. Although the present analysis is limited to a single site, similar patterns of temperature variability have been observed in a shorter time series from Looe Key in the lower Florida Keys (Lapoint and Smith, 1987), and at reef sites throughout the Florida Keys from 1996 to 1998 (Leichter, unpublished data). Thus, high-frequency upwelling may be a widespread and important phenomenon on reefs throughout the Florida Keys.

2. Methods

Conch Reef, FL (24°59′ N, 80°25′ W) is a Holocene fringing reef lying along the submerged Pleistocene margin of Key Largo (Shinn et al., 1989) in the upper Florida Keys (Fig. 1). Small (1–2 m height) coral spur and groove formations run down the fore reef from a depth of approximately 12–30 m where the formations break up into isolated patches on coral sand. A mixture of hard and soft corals, sponges, and benthic algae dominates space on the reef. At approximately 35 m the reef ends on a gently sloping sand plain that extends 8–10 km to the deep channel of the Florida Straits. This bottom slope is characterized by roughly 10–20 m increase in depth per 1 km distance offshore to a depth of 300 m where the slope angle increases into the deep channel (800–1200 m depth at 70–100 km offshore) of the Florida Straits. Surface tides in the upper Florida Keys are mixed semi-diurnal with mean amplitude of 0.25–0.75 m.

Temperature data on Conch Reef were collected nearly continuously from 1992–1997 at 21 and 33 m depth, and throughout 1992 at 7 m and 1997 at 10 m. At 7, 21, and 33 m Ryan Tempmentors were fixed 1 m above the bottom recording at 20 min intervals for deployments of up to 3 months. An Onset Computers Stowaway meter in a waterproof pressure housing and configured for rapid response times ($<$20 s to temperature changes of 5°C (Leichter et al., 1998)) was fixed 1 m above the

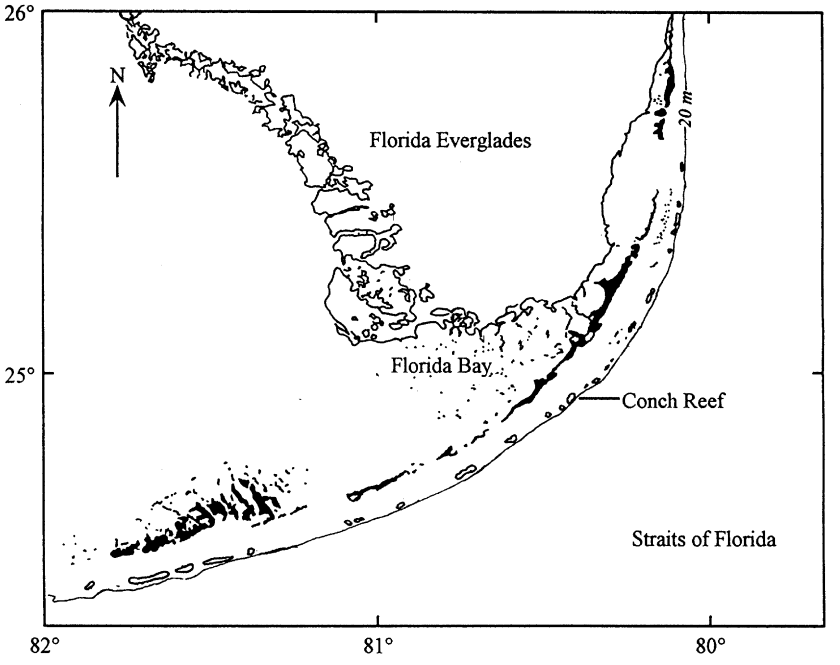

Fig. 1. Map of S. Florida, with the Florida Keys and offshore reef track including Conch Reef (24°59′ N, 80°25′ W). The approximate location of the 20 m bathymetric contour seaward of the reef track is indicated.

bottom at 10 m depth from December 1996–1997. Time series analysis was employed to examine periodicity of temperature fluctuations in the continuous data record from 33 m for November 1994–November 1997. Low-frequency, seasonal variation was first removed by subtracting a centered 90-day moving average, and a power spectrum was calculated after fast Fourier transformation (FFT) of the residual data (Chatfield, 1989). A smoothed power spectrum was produced by Welch's method of averaging replicate spectra calculated on a series of non-overlapping 8192-point (114-day) sections of the data using the computer program MATLAB 5.1 (MathWorks 1997).

For each day in the temperature records from 7, 21, and 33 m the mean, standard deviation, minimum, maximum, and range (maximum–minimum) were calculated. Monthly (31 day) means were also calculated. Daily minimum temperature anomalies were calculated as the difference between the daily minimum temperature and the monthly mean temperature (31-day centered moving average) for each day. The distributions of extreme values in the daily minimum temperature anomaly records were examined following the methods of Gumbel (1958), Jacocks and Kneile (1975), and Galambos (1987) as outline in Denny and Gaines (1990) and Gaines and Denny (1993). The principle of this analysis is to (1) divide the time series into a series of equal length intervals, (2) record the extreme value in each interval, (3) rank these extreme values in ascending order (tied values are given a mean rank) and (4) fit a continuous probability function to their cumulative distribution. This cumulative probability

function, $P(x)$, describes the chance that the magnitude of the extreme value, x_i, in a single interval will be less than or equal to a given value of x:

$$P(x) = \text{Prob}(x_i \leqslant x). \tag{1}$$

The inverse of $1 - P(x)$, $\tau(x)$, describes the median (most probable) number of sample intervals that will elapse between successive occurrences of a given extreme value x:

$$\tau(x) = 1/(1 - P(x)), \tag{2}$$

where $\tau(x)$ is the median return time (in days) for the extreme value x. If the extreme values are independent and identically distributed (i.e. the distribution of extreme values is unchanging through time), and N is reasonably large (>20), the cumulative probability function approaches an asymptotic form described by Jacocks and Kneile (1975):

$$P(x) = \exp -[(\alpha - \beta x)/(\alpha - \beta\varepsilon)]^{1/\beta}, \tag{3}$$

where α measure the rate of increase of $P(x)$ with the natural logarithm of time, the ratio of α/β estimates the maximum achievable extreme value (when α and β are both >0), and ε is the most frequently occurring extreme value (the mode) (Denny and Gaines, 1990). Lagged autocorrelations of the anomaly data at lags of 5–10 days were non-significant. To ensure serial independence, the anomaly data were re-sampled for the extreme values in 10-day intervals. Because temperatures at 21 and 33 m were most variable during summer months (i.e. the variation in temperature varied seasonally) the anomaly data for each depth were divided into records for each of two seasons: May 1–September 30 ('Summer'), and October 1–April 30 ('Winter').

Estimates of α, β, and ε in Eq. (3) were found by maximum likelihood, nonlinear curve fitting in the computer program Systat 6.01 (Systat Inc., 1996). R^2 values from linear regression between observed values and values predicted by the fitted probability function were examined as an estimate of goodness of fit.

The durations of cold temperature anomaly events from 1992–1997 at 21 and 33 m depths were also examined. Temperature anomaly values were calculated by subtracting monthly means (31-day centered moving average) from the 20 min sample interval data. Durations for anomaly events at 0.5°C intervals from -1 to -7.5°C were then determined with a computer program that scanned the 20 min interval data files recording the length (number of sample intervals) of each event where temperature dropped below a given anomaly value. Means and standard errors for each value of the temperature anomaly were calculated from the resulting list of event durations.

3. Results

The general patterns of near-bottom temperatures at Conch Reef were similar across the six years of study – consistent seasonal trends of summer warming to near 30°C and winter cooling to the low 20°C set a background for extensive, higher frequency variation. Fig. 2 shows the entire temperature records for 7, 21, and 33 m. Table 1 presents temperature summary statistics for each depth for the Summer

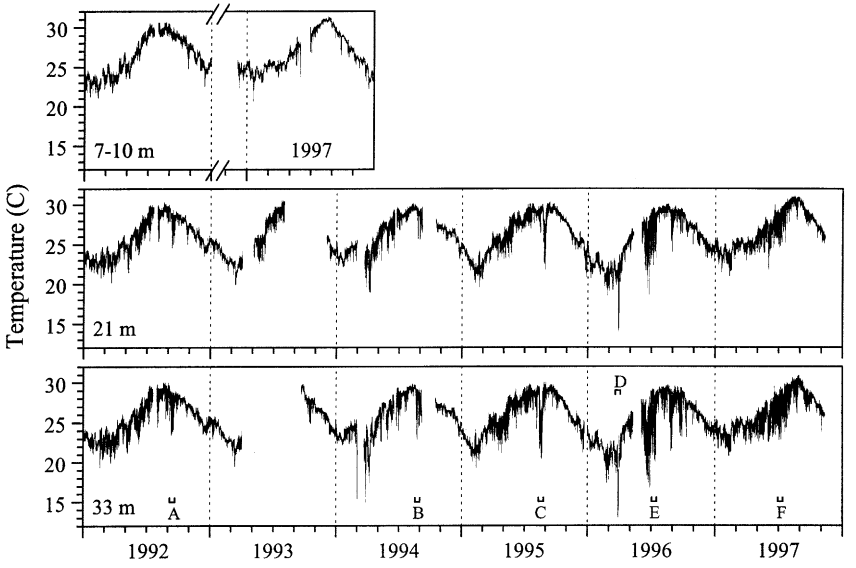

Fig. 2. Temperature recorded 1 m above the bottom at 20 min intervals at 7–10, 21, and 33 m depth on Conch Reef, 1992–1997. Lettered sections from 33 m record are expanded in Fig. 3.

Table 1
Conch Reef temperature summary for Summer (May–September) and Winter (October–April) 1992–1997

Depth (m)	Season	Mean (°C)	Std	Min	Max	Range	N
7–10	S	28.7	1.6	23.6	31.3	7.7	269
21	S	28.1	1.5	18.6	31.1	12.5	790
33	S	27.3	1.7	16.8	30.9	14.1	711
7–10	W	25.2	1.5	20.5	29.2	8.7	456
21	W	24.6	1.9	13.9	29.7	15.8	1118
33	W	24.4	2.1	13.0	29.7	16.7	1100

(May–Sept) and Winter (October–April) seasons. Mean temperatures were approximately 3–3.5°C lower in Winter than Summer at all depths. Minimum temperatures were lowest at the deepest site, and temperature ranges were greatest at the deepest site. At 21 and 33 m the maximum within-day temperature ranges were 9.9 and 10.6°C, respectively. These within-day temperature ranges represent 58 and 59% of the overall temperatures ranges recorded for the entire six-year study period. Periods of extensive temperature variation and corresponding large negative minimum temperature anomalies were recorded in the summer of each year as well as in March of both 1994 and 1996. Fig. 3 shows six expanded, 14-day sections of highly variable portions of the temperature record for 33 m. Highly variable temperature conditions at 33 m consisted variously of series of semi-independent rapid cold spikes lasting 1 to

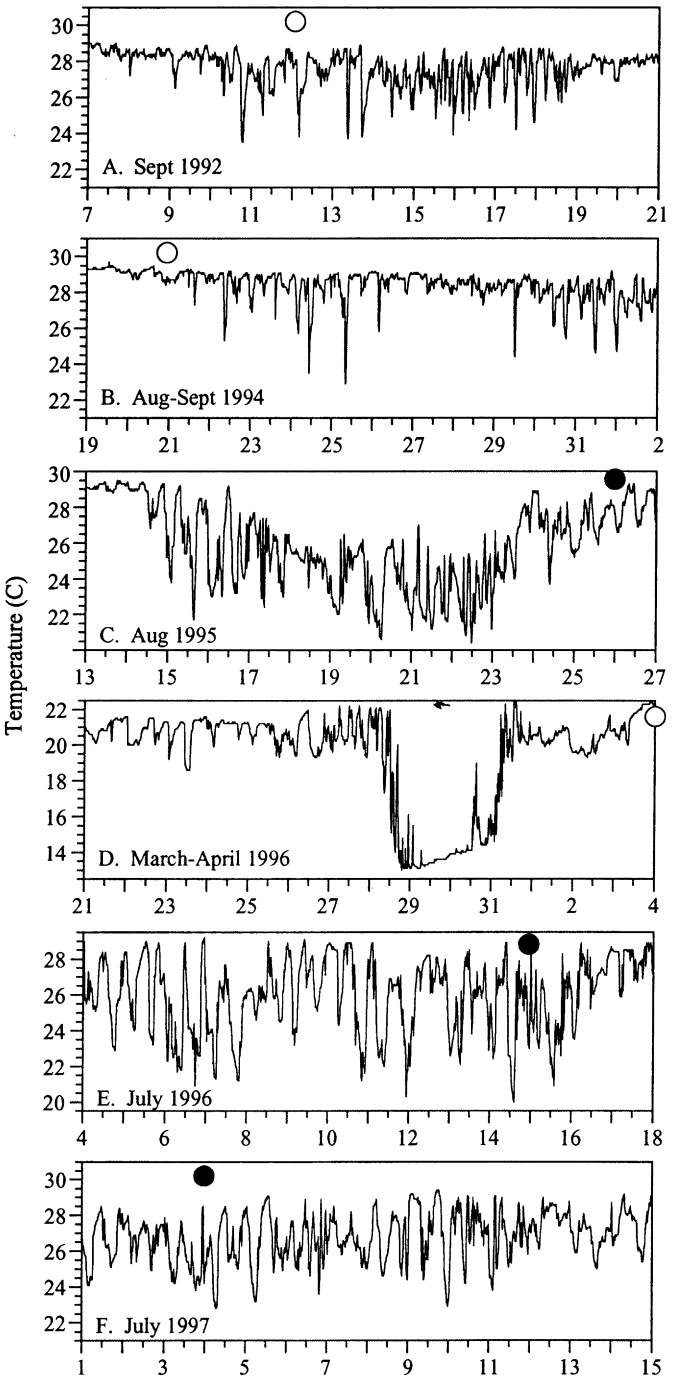

Fig. 3. 14-day sections of the temperature record from 33 m depth. (A) Sept 7–21, 1992; (B) Aug 19–Sept 2, 1994; (C) Aug 13-27, 1995; (D) Mar 21–Apr 4, 1996; (E) July 4–18, 1996; (F) July 1–15, 1997.

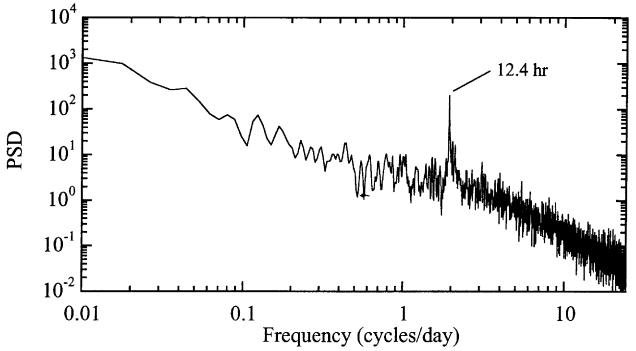

Fig. 4. Power spectrum for temperature record from 33 m depth. Smooth spectrum produced by Welch's method of averaging replicate spectra calculated on a series of non-overlapping 8192 point data sections.

several hours (Fig. 3 panels A and B), as periods of overall cooling lasting several days and accompanied by numerous rapid fluctuations (panels C and D), and as periods of large temperature oscillations at predominantly semi-daily periods (panels E and F). Highly variable temperature conditions were often, but not exclusively, associated with days close the full or new moon when tidal amplitudes are greatest. Fig. 4 shows the power spectrum for data from 33 m at frequencies corresponding to periods of 100 days–2 h. A single significant spectral peak is evident at a frequency corresponding to a period of 12.4 h.

Fig. 5 shows calculated daily minimum temperature anomaly values at 7, 21, and 33 m for the entire study period. Fig. 6 shows frequency distributions for the minimum temperature anomalies at each depth for May–September and October–April over the entire study period. At both 33 and 21 m the distributions show a shift in Summer to a relatively larger proportion of observations occurring at large negative minimum temperature anomalies. At 7 m this shift did not occur and the shapes of the distribution of anomaly observations are similar between Summer and Winter. Cumulative probability distributions with fitted continuous probability functions for the Summer and Winter daily minimum temperature anomaly data are shown in Fig. 7, left column. Coefficients of linear regression for predicted vs observed values were all $\geqslant 0.991$, indicating excellent fits of the fitted probability functions to the measured data. The overall shapes of the probability functions are similar across depths, however, the location of the modes differ among depths and the proportion of values at large anomalies is lowest at 7 m and increases from 21 to 33 m. For both 33 and 21 m the relative fraction of observations of large negative anomalies is markedly greater in Summer than in Winter. Fig. 7, right column, and Table 2 show predicted median return times for daily minimum temperature anomalies for the Summer and Winter at all three depths. Return times show large differences among depths and seasons with far longer predicted return times at 7 and 21 m than at 33 m especially for large magnitudes of the daily minimum temperature anomaly. For example, the median return times for -2°C minimum temperature anomaly are 3, 6, and 35 days at 33, 21, and 7 m, respectively, in Summer, and 12, 16, and 38 days at 33, 21, and 7 m

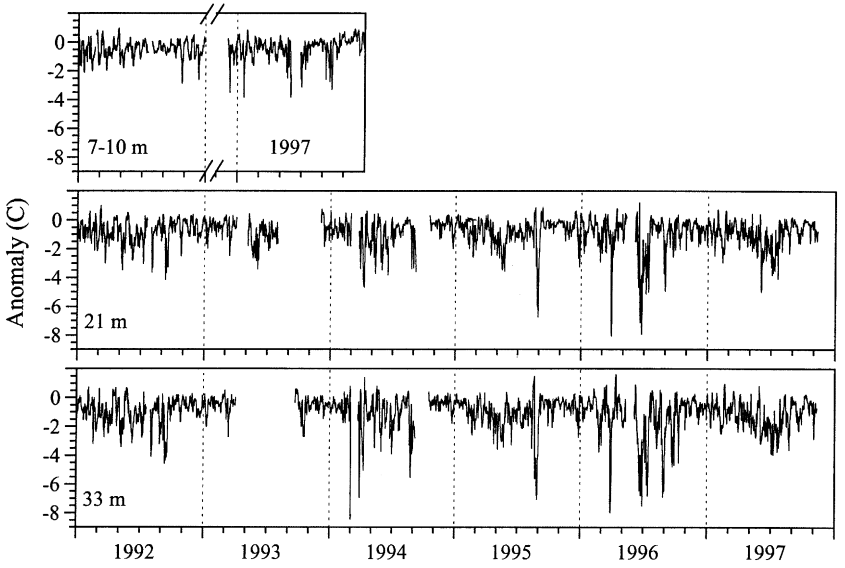

Fig. 5. Daily minimum temperature anomalies (daily minimum temperature minus 31-day mean temperature) at 7–10, 21, and 33 m depth 1992–1997.

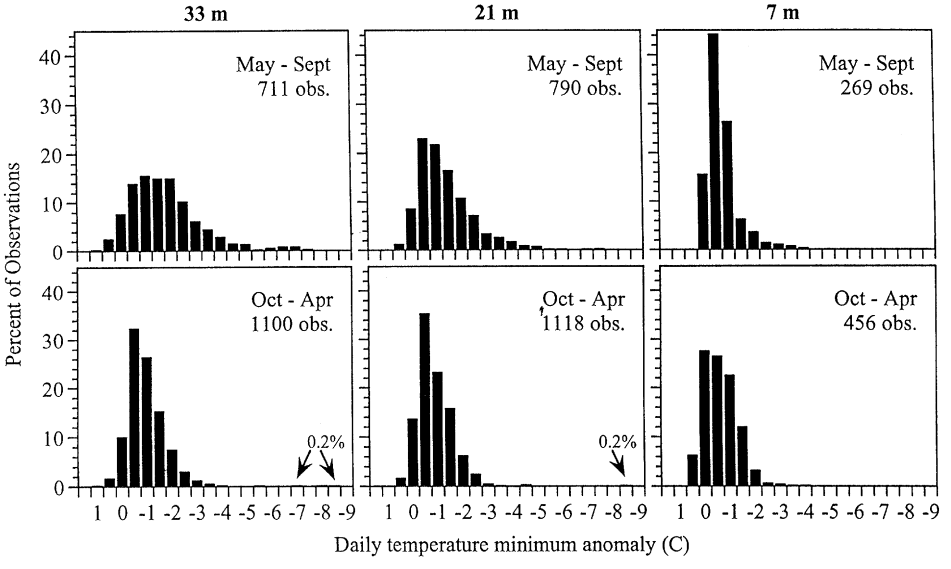

Fig. 6. Overall frequency distributions of the daily minimum temperature anomalies in Summer (May–September) and Winter (October–April) at 7–10, 21, and 33 m depth for 1992–1997.

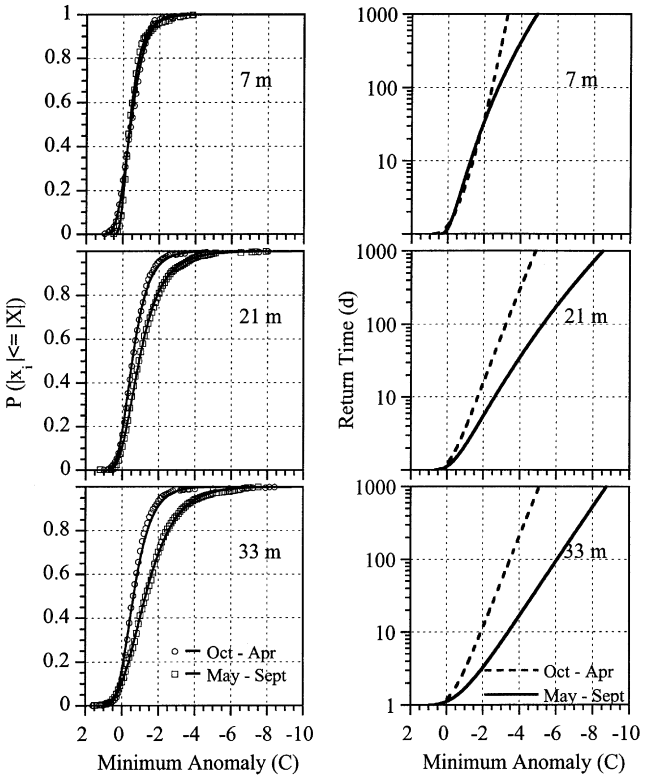

Fig. 7. Cumulative probabilities for daily minimum temperature anomalies (left column). Open symbols represent observed values (open circles October–April, open squares May–September), solid line curves are maximum likelihood fits of continuous probability functions. Return times (right column) calculated from continuous probability functions (dashed lines October–April, solid lines May–September).

in Winter. For a -4°C minimum temperature anomaly the median return times increase to 17, 35, and 423 days in Summer and 210, 307, and >1000 days at 33, 21, and 7 m in Winter. Return time calculations can also be used to predict the magnitude of the extreme minimum temperature anomaly that would be likely to be observed over a given exposure period at each depth. Table 3 shows predicted extreme minimum temperature anomaly values for exposure periods of 10, 100, and 1000 days.

Fig. 8 shows calculated event durations as a function of temperature anomalies from -1 to -7.5°C. At each anomaly magnitude, more events were observed at 33 than at 21 m. The mean durations of cool water events were approximately 120–150 min at 33 m and 40–100 min at 21 m. At 33 m both the mean and the variance of event durations increase with increasing magnitude of the temperature anomaly from -4 to -7°C. This implies that the largest magnitude anomaly events are associated with cooling on a longer time scale (hours to days) than are small magnitude anomaly events which are associated with cooling on an hourly time scale.

Table 2
Predicted median return times (days) for minimum temperature anomalies from −2 to −8°C at 7, 21, and 33 m depth for Summer (May–September) and Winter (October–April)

	Summer Depth (m)		
Anomaly (°C)	7	21	33
−2	35	6	3
−3	136	14	7
−4	423	35	17
−5	*	82	40
−6	*	178	95
−7	*	367	224
−8	*	720	530
	Winter Depth (m)		
Anomaly (°C)	7	21	33
−2	38	16	12
−3	469	72	49
−4	*	307	210
−5	*	*	892
−6	*	*	*

* indicates return times >1000 days.

Table 3
Predicted extreme values (°C) for daily minimum temperature anomaly at exposure periods (return times) from 10 to 1000 days

	Exposure Period (d)		
	10	100	1000
Summer			
7 m	−0.9	−2.8	−4.9
21 m	−2.6	−5.3	−8.5
33 m	−3.4	−6.0	−8.8
Winter			
7 m	−1.0	−2.4	−3.0
21 m	−1.7	−3.2	−4.8
33 m	−1.9	−3.5	−5.1

4. Discussion

The observation of upwelling on coral reefs in general, and on reefs in the Florida Keys in particular, is not without precedent. Sporadic upwelling may be an important source of nutrients for reefs along the outer Great Barrier Reef (Andrews and Gentien, 1982; Wolanski and Pickard, 1983; Wolanski, 1994), the Seychelles Islands

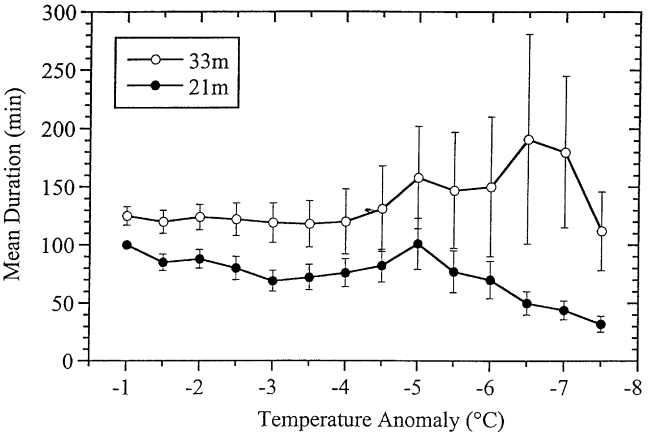

Fig. 8. Mean duration of temperature anomaly events at 21 and 33 m for 1992–1997. Error bars represent 1 standard error of the mean.

(Novozhilov et al., 1992), the Gulf of Oman (Quinn and Johnson, 1996), the lower Florida Keys (Lapoint and Smith, 1987), and other sites that lie in close proximity to deep water and strong thermal/density stratification. However, while previous studies have be confined to relatively short time series (weeks to months) the present six-year study provides an unprecedented, long time series of high frequency, near bottom observations. For the upper Florida Keys this provides a view of upwelling not as isolated, rare events, but as a persistent, predictable aspect of the physical environment.

From 1992–1997 water temperatures on Conch Reef were highly variable on a range of time scales from minutes to seasons. While long-term (seasonal to annual) patterns consist of predictable summer warming and winter cooling within a relatively limited (6–8°C) range of monthly mean temperatures, strong signals of high frequency variation are superimposed on these low-frequency patterns. Temperature variation increases with increasing depth from 7 to 33 m, and temperature at 33 m can change 5–9°C within 20 min. Conditions often vary nearly as much within individual days as across entire years. Close examination of highly variable portions of the overall temperature record suggests that extensive temperature fluctuations can be driven by a variety of mechanisms. The sudden, semi-independent temperature drops of as much as 6°C often followed by more gradual warming (e.g. Fig. 3 panels A and B) represent a characteristic temperature signal of internal bores arriving on the reef slope. Internal bores produce pulses of cool water on the reef slope at roughly semi-diurnal frequencies with durations of one to several hours (Leichter et al., 1996). During these events, rapid drops in temperature are accompanied by sharp increases in flow speed, and in concentrations of nutrients, chlorophyll *a*, and zooplankton (Leichter et al., 1996, 1998). The alongshore spatial scale of internal bores is unknown, but may be on the order of one to several kilometers (Leichter et al., 1996). Patterns of high frequency temperature variation should be modulated by offshore processes associated with

meanders and eddies of the Florida Current. There is also strong seasonal modulation of internal tidal forcing associated with summer warming and increased density stratification of the thermocline.

The pronounced cooling periods lasting several days or more (e.g. Fig. 3 panels C and D) likely represent subsurface intrusions of cool water onto the shelf seaward the reef. Upwelling on a scale of days to weeks can occur between offshore Florida Current meanders and the reef shelf. Upwelled water may travel alongshore, downstream with the mean flow as cool, cyclonic eddies (Atkinson, 1977; Lee et al., 1981; Lee and Atkinson, 1983; Zantopp et al., 1987; Lee et al., 1992, 1994, 1995). The spatial scale of such events may be on the order of 10s of kilometers, and sites along the Keys reef track may show correlated periods of upwelling. Cooling due to passing weather events, or outflow of cold water from the Florida Bay in Winter do not represent upwelling of deep, nutrient rich water, and are an unlikely explanation of the large temperature changes observed as deep as 20–30 m on Conch Reef. However wind forcing may interact with Florida Current variability to produce upwelling (Lapoint and Smith, 1987). As cool subsurface water is forced onshore below warmer surface water, the strength of the density gradient at the thermocline/pycnocline should increase, with accompanying periods of extensive internal tidal activity (e.g. Fig. 3 panel C). Temperature fluctuations as large as 5–9°C can also occur at reasonably regular tidal intervals (e.g. Fig. 3 panels E and F), likely caused by vertical oscillations of the thermocline under the influence of semi-diurnal internal tides. Hydrographic sampling seaward of Conch Reef (Leichter et al., 1996, 1998) has consistently shown a well defined thermocline/pycnocline at depths between 50 and 80 m capable of supporting internal tides and internal waves. This thermocline also corresponds to a marked subsurface chlorophyll *a* maximum layer and nutricline. In August 1995 temperatures above 28.5°C were associated with chlorophyll *a* concentrations less than 0.6 mg l^{-1}, while temperatures of 21–24°C were associated with increased chlorophyll *a* concentrations from 1.5 to 1.85 mg l^{-1}. Below the thermocline chlorophyll *a* concentrations are generally low in association with 12–15°C water at 100 m and deeper. Lapoint and Smith (1987), Lee et al., (1994) and Leichter et al., (1996) have all reported sharply increasing concentrations of NO_3^- and PO_4^{3-} in subthermocline waters seaward of the Florida Keys.

The long-term observations suggest that mechanisms of upwelling in the vicinity of Conch Reef can interact to produce temperature variability at a range of time scales. However, spectral analysis also clearly shows that temperature variability on the reef slope is concentrated at the 12.4 h semi-diurnal internal tidal period. The interpretation that temperature variability is driven by mechanisms associated with M2 internal tidal phenomena is not exclusive of other lower frequency mechanisms. Rather, events such as cool water intrusions appear not to occur with regular periodicity that would produce spectral peaks in the frequency domain. Lower frequency upwelling mechanisms are likely to be particularly important for large-scale events with long return times.

Spectral analysis provides limited information on the magnitude of forcing events. However, the analysis of extreme temperature anomaly values provides quantitative, site-specific predictions of the median return times for upwelling events as a function

of the magnitude of temperature changes. The distributions of temperature extremes (Figs. 6, 7) differ markedly both between seasons and across depths, reflecting greater rates of cool water arrival in Summer than in Winter and increasing exposure to cool water with increasing depth on the reef slope. Return times predictions represent a probability statement regarding the most likely number of days that will elapse between successive occurrences of cooling events of a given magnitude. In Summer, for example, the median return times for a -3°C anomaly are 136, 14, and 7 days at 7, 21, and 33 m depths, respectively (Table 2). During the time it would take for one such cooling event to be observed at 7 m, 9 events of this magnitude would be observed at 21 m and 19 would be observed at 33 m. In Winter the return times for events of the same magnitude increase to 469, 72, and 49 days at 7, 21, and 33 m. Long return times such as 469 days at 7 m suggest that events of this magnitude will occur very infrequently even over several Winter seasons. The methods utilized here provide a quantitative means of comparing near-bottom temperature variability among sites and through time in a metric – the expected number of days between extreme events – that is directly relevant to wide a range of physiological, ecological, and oceanographic questions. Further, because temperature changes can be closely associated with changes in nutrient, chlorophyll *a* and zooplankton concentrations, the long-term temperature records can be used in predicting return times for transport to the reef of nutrients, suspended particles, and planktonic larvae.

The statistics of extremes employed here depend on assumptions that the extreme values are independent and identically distributed. Independence was achieved by examining lagged autocorrelations and re-sampling the data for the extreme values at 10-day intervals, corresponding to lags at which the autocorrelations were not significantly different from zero. Where autocorrelation functions decrease rapidly with increasing lag, fitted cumulative probability functions have been shown to be relatively insensitive to re-sampling interval (Gaines and Denny, 1993). The assumption of identical distribution (that the overall distribution of extreme values is unchanging through time) is particularly important where predictions for return times of extreme values exceeding those actually observed are of most interest. For certain mechanical systems, where it is known that extreme values are truly identically distributed, it is possible to predict critical extreme values at return times far longer than the sampling duration (Jacocks and Kneile, 1975). In this study, long-term seasonal trends which cause the data clearly to deviate from identical distributions where removed by subtracting long-term running averages as well as by dividing the data into Winter and Summer seasons. While extrapolation of the return times to anomaly values outside the range actually observed is probably not justified, for the range of observed anomalies and for return times within the range of the sampling period (1–1000 days), the predicted median return times are likely to be quite reliable.

Both the long-term records and predicted return times for cool water anomalies show that rapid cooling on the reef is not exclusively a Summer phenomenon. For a period of several days in March 1996 near-bottom temperatures were as cold as 13.1°C at 33 m and 15.9°C at 21 m. A similar period of extreme cool temperatures near 15°C was observed in March of 1994. These extremely cool periods, and the period in August 1995 when temperatures fell into the low 20 s for several days likely represent

large-scale intrusions of deep water onto the shelf. The six-year data set suggests there has been no change in the annual mean or the maximum observed temperatures, but does show that minimum observed temperatures were considerably colder in 1996 than in other years. Summer temperatures were particularly variable in 1996, a year with an unusually large number of hurricanes and tropical storms in the western Atlantic and Caribbean. Large storm events may trigger periods of intense internal tidal activity and associated near-bottom temperature variability at Conch Reef (Wing and Leichter, 1996). By contrast, in Summer 1997 mean near-bottom temperatures were the highest observed in the six-year study period, and temperature variation was reduced. 1997 was a year with an unusually small number of large storms in the western Atlantic and Caribbean.

The biological and potential ecological effects of high-frequency upwelling in the Florida Keys are not well understood. Extreme upwelling and associated temperature variability are known to be problematic for hermatypic corals (Glynn, 1993), and coral mortality on Florida reefs have been reported when temperatures have fallen below 15°C for periods of a few days (Shinn, 1966; Hudson, 1981; Davis, 1982; Porter et al., 1982). Repeated upwelling caused by intrusions of deep water onto the shelf may have contributed to relatively slow rates of Holocene reef accretion in the Keys compared with other sites in the Caribbean (E. Shinn personal communication). The present analysis shows that temperatures at Conch Reef frequently drop into the low 20°C, reach the upper teens occasionally, and can drop as low as 13°C for periods of several days. Conch Reef lies near the upper latitudinal distribution limit for hermatypic corals in the Western Atlantic. Return times for cold water anomalies suggest that, over the decadal to centennial time scales representative of coral colony life spans and the development of reefs, problematic low temperatures are likely to be a common occurrence on Conch Reef. Yet, this and nearby sites in the Florida Keys do support relatively high density and diversity of hermatypic corals. Persistent, intermediate levels of high frequency upwelling may, in fact, represent an important source of allochthonous (externally-derived) nutrients and suspended particles that contribute significantly to productivity on Conch Reef (Leichter et al., 1998). Duration of exposure may be as important as the magnitude of temperature anomalies in determining biological effects. The mean durations of cool water events calculated here are on the scale of 60–180 min and maximum durations were more than an order of magnitude larger.

5. Conclusions

Long-term, high-frequency data reveal a highly variable temperature regime on the slope of Conch Reef, Florida Keys. While temperature variability is concentrated at semi-diurnal internal tidal frequencies, upwelling of subsurface water onto the reef slope can occur on a range of time scales. Upwelling appears to be produced through interaction of mechanisms associated with internal tidal forcing and variability of the Florida Current. The later likely includes offshore current meanders and passing cyclonic eddies. Predicted return times for cold temperature anomalies reveal

significant spatial variability across the reef slope in the frequency and magnitude of cooling events. The greatest temperature variability and shortest return times for upwelling events are found at the deepest site. The observation of persistent upwelling and associated cold temperature extremes emphasizes the fundamental interaction between the benthic physical variability on this Florida coral reef and the surrounding oceanographic environment. Understanding oceanographic mechanisms behind spatial and temporal patterns of physical variability should facilitate a range of biological and ecological investigations and lead to a more complete understanding of the ecology of Florida Keys coral reefs.

Acknowledgements

We thank O. Rutten, T. Potts, and the entire staff of the National Undersea Research Center, Key Largo FL. Mark Denny provided assistance in the application of statistics of extremes. Comments by two anonymous reviewers significantly improved the manuscript. This research was supported through grants from the National Undersea Research Program at the University or North Carolina at Wilmington. This is W.H.O.I. contribution 9871.

References

Andrews, J.C., Gentien, P., 1982. Upwelling as a source of nutrients for the Great Barrier Reef ecosystem: a solution to Darwin's question? Marine Ecology Progress Series 8, 257–269.

Atkinson, L.P., 1977. Modes of Gulf Stream intrusion into the South Atlantic Bight shelf waters. Geophysics Research Letters 4, 583–586.

Atkinson, L.P., Blanton, J.O., 1986. Processes that affect stratification in shelf waters. In: Moores, N.K. (Ed.), Processes that Affect Stratification in Shelf Waters. AGU, Washington, DC, pp. 117–130

Blanton, J.O., Atkinson, L.P., Pietrafesa, L.J., Lee, T.N., 1981. The intrusion of Gulf Stream water across the continental shelf due to topographically-induced upwelling. Deep Sea Research 28, 393–405.

Chatfield, C., 1989. The Analysis of Time Series, 4th ed. Chapman & Hall, London.

Coles, S.L., Fadlallah, U.H., 1991. Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. Coral Reefs 9, 231–237.

Dana, J. D., 1843. On the temperature limiting the distribution of corals. American Journal Science 45, 130–131.

Davis, G.E., 1982. A century of natural change in coral distribution at the Dry Tortugus: a comparison of reef maps from 1881–1976. Bulletin Marine Science 32, 608–623.

Denny, M.W., Gaines, S.D., 1990. On the prediction of maximal intertidal wave forces. Limnology and Oceanography 35, 1–15.

Gaines, S.D., Denny, M.W., 1993. The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. Ecology 74, 1677–1692.

Galambos, J., 1987. The Asymptotic Theory of Extreme Order Statistics. Robert E. Krieger, Malabar, FL, USA.

Glynn, P.W., Stewart, R.H., 1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. Limnology and Oceanography 18, 367–379.

Glynn, P.W., Wellington, G.M., 1983. Corals and Coral Reefs of the Galapagos Islands. Univ. California Press, Berkeley, Berkeley, CA.

Glynn, P.W., D'Croz, L., 1990. Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. Coral Reefs 8, 181–191.
Glynn, P.W., 1991. Coral reef bleaching in the 1980s and possible connections with global warming. Trends Ecology and Evolution 6, 175–179.
Glynn, P.W., 1993. Coral reef bleaching: ecological perspectives. Coral Reefs 12, 1–17.
Green, C., 1944. Summer upwelling – northeast coast of Florida. Science 100, 546–547.
Gumbel, E.J., 1958. Statistics of Extremes. Columbia Univ. Press, New York.
Hudson, J.H., 1981. Response of Montastrea annularis to environmental change in the Florida Keys. Proceedings of the 4th Internstionsl Coral Reef Symposium, Vol. 2, pp. 233–240.
Jacocks, J.L., Kneile, K.R., 1975. Statistical prediction of maximum time-variant inlet distortion levels. Arnold Engineering Development Center Technical Report AD/A–004. National Technical Information Service, US Dept. Commerce, Washington, DC, USA.
Jokiel, P.L., Coles, S.L., 1977. Effects of temperature on the mortality and growth of Hawaiian reef corals. Marine Biology 43, 201–208.
Jokiel, P.L., Coles, S.L., 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs 8, 155–162.
Lee, T.N., Atkinson, L.P., Legekis, R., 1981. Observations of a Gulf Stream frontal eddy on the Georgia continental shelf, April 1977. Deep-Sea Research. 28A, 347–378.
Lee, T.N., Atkinson, L.P., 1983. Low-frequency current and temperature variability from Gulf Stream frontal eddies and atmospheric forcing along the southeast U.S. Outer Continental Shelf. Journal of Geophysical Research 88(C8), 4541–4568.
Lee, T.N., Schott, F.A., Zantopp, R., 1985. Florida Current: low-frequency variability as observed with moored current meters during April 1982 to June 1983. Science 227, 298–302.
Lee, T.N., Rooth, C., Williams, E., McGowan, M., Szmant, A.F., Clarke, M.E., 1992. Influence of Florida Current, gyres and wind-driven circulation on transport of larvae and recruitment in the Florida Keys coral reefs. Continental Shelf Research 12, 971–1002.
Lee, T.N., Clarke, M.E., Williams, E., Szmant, A.F., Berger, T., 1994. Evolution of the Tortugas gyre and its influence on recruitment in the Florida Keys. Bulletin Marine Science 54, 621–646.
Lee, T.N., Leaman, K., Williams, E., Berger, T., Atkinson, L., 1995. Florida Current meanders and gyre formation in the southern Straits of Florida. Journal of Geophysical Research 100, 8607–8620.
Leichter, J.J., Wing, S.R., Miller, S.L., Denny, M.W., 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. Limnology and Oceanography 41, 1490–1501.
Leichter, J.J., Shellenbarger, G., Genovese, S.J., Wing, S.R., 1998. Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? Marine Ecology Progress Series 166, 83–97.
Mann, K.H., Lazier, J.R.N., 1996. Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans. Blackwell, Cambridge, MA.
Mayor, A.G., 1916. The lower temperature at which reef corals lose their ability to capture food. Abstracts Carnegie Institute Washington 14, 212.
Novozhilov, A.V., Chernova, Y.N., Tsukurov, I.A., Densiov, V.A., Propp, L. N., 1992. Characteristics of oceanographic processes on reefs of the Seychelles Islands. Atoll Research Bulletin 366, 1–36.
Porter, J.W., Battey, J.F., Smith, J.G., 1982. Perturbation and change in coral reef communities. Proceedings National Academy of Sciences USA 79, 1678–1681.
Quinn, N.J., Johnson, D.W., 1996. Cold water upwellings cover Gulf of Oman coral reefs. Coral Reefs 15, 214.
Shinn, E.A., 1966. Coral growth rate, an environmental indicator. Journal of Paleontology 40, 233–240.
Smith, N.P., 1982. Upwelling in Atlantic Shelf water of South Florida. Florida Scientist 45, 125–138.
Smith, N. P., 1983. Temporal and spatial characteristics of summer upwelling along Florida's Atlantic Shelf. Journal of Physical Oceanography 13, 1709–1715.
Taylor, C., Stewart, H.B., 1957. Summer upwelling along the east coast of Florida. Journal of Geophysical Research 64, 33–39.
Tomascik, T., Sander, F., 1987. Effects of eutrophication on reef-building corals. 2: Structure of scleractinian coral communities on fringing reef, Barbados, West Indies. Marine Biology 94, 53–75.

Veron, J.E.N., 1995. Corals in Space and Time. The Biogeography and Evolution of the Scleractinia. Univ. New South Wales Press, Sydney.

Wing, S.R., Leichter, J.J., 1996. Storm-generated physical variability on Conch Reef, Florida Keys, U.S.A. Proceedings of 8th International Coral Reef Symposium, vol. 2, pp. 1097–1102.

Wolanski, E., 1994. Physical oceanographic processes of the Great Barrier Reef. CRC, Boca Raton.

Wolanski, E., Pickard, G.L., 1983. Upwelling by internal tides and Kelvin waves at the continental shelf break on the Great Barrier Reef. Austtralian Journal of Marine Research 34, 65–80.

Yonge, C.M., 1940. The biology of reef-building corals. British Museum (Natural History), Science Reports Great Barrier Reef Exped. 1928–1929. Vol. 1, pp. 353–391.

Zantopp, K.D., Leaman, K.D., Lee, T.N., 1987. Florida Current meanders: a close look in June–July 1984. Journal of Physical Oceanography 17, 584–595.